Fall 2016

ENVIRONMENTAL VARIABLES ASSOCIATED WITH INVASIVE GLOSSY BUCKTHORN (FRANGULA ALNUS MILL.) AND INDIRECT CONTROL STRATEGIES FOR FOREST MANAGERS

JOSHUA GLIDDEN KOZIKOWSKI
University of New Hampshire, Durham

ENVIRONMENTAL VARIABLES ASSOCIATED WITH INVASIVE GLOSSY BUCKTHORN (*FRANGULA ALNUS* MILL.) AND INDIRECT CONTROL STRATEGIES FOR FOREST MANAGERS

BY

JOSHUA GLIDDEN KOZIKOWSKI
Bachelor of Science in Forestry, Minor in Wildlife and Conservation Biology
University of New Hampshire, 2014

THESIS

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Master of Science
in
Natural Resources: Forestry

September 2016

This thesis has been examined and approved in partial fulfillment of the requirements for the degree of Master of Science in Natural Resources: Forestry by:

Dr. Theodore E. Howard, Thesis Director
Professor, Natural Resources and The Environment

Dr. Mark J. Ducey
Professor, Natural Resources and The Environment

Dr. Thomas D. Lee
Associate Professor, Natural Resources and The Environment

William B. Leak
Research Forester, USDA Forest Service

7/15/16
Date

Original approval signatures are on file with the University of New Hampshire Graduate School

ACKNOWLEDGMENTS

This project would not have been possible without the assistance and support of my amazing committee – Dr. Ted Howard, Dr. Tom Lee, Dr. Mark Ducey, and Bill Leak. Their vast knowledge, insight, thoughtful questions, and belief in me are much appreciated. Specifically I would like to thank Dr. Ted Howard. He offered me the opportunity and, under his guidance and trust, I was able to accomplish something I am very proud of.

I would also like to thank the landowners and managers for the use of their properties for sampling. Lastly I would like to thank my friends and family for their support over the last two years.

Table of Contents

LIST OF TABLES

LIST OF FIGURES

LIST OF EQUATIONS

ABSTRACT

ENVIRONMENTAL VARIABLES ASSOCIATED WITH INVASIVE GLOSSY BUCKTHORN (*FRANGULA ALNUS* MILL.) AND INDIRECT CONTROL STRATEGIES FOR FOREST MANAGERS

by

Joshua Glidden Kozikowski

University of New Hampshire, September 2016

Glossy buckthorn (*Frangula alnus* Mill.) is one of the most prominent non-native invasive plant species affecting New England forests. It quickly invades a forest and can create a dense understory effectively altering the species composition and dynamics of that forest. To gain a better understanding of the environmental variables associated with glossy buckthorn density we sampled forests across New Hampshire with varying degrees of buckthorn invasion. The effect on tree regeneration was analyzed with measurements of height and abundance of glossy buckthorn and native regeneration. Glossy buckthorn was found to be at its highest densities in disturbed softwood forests that were historically old fields, specifically eastern white pine (*Pinus strobus* L.), with a thin organic layer and low herbaceous cover on drained loam and clay soils. The data show there is direct competition between glossy buckthorn and forest tree regeneration, although no relationship with regeneration shade tolerance was found. This information was used to create a prescription risk tree to aid forest managers in assessing the risk of buckthorn invasion and inhibition of tree regeneration associated with harvesting and suggests how to adapt their silvicultural prescriptions.

CHAPTER I

Introduction

While native tree species have been in New England for thousands of years, nonnative invasive woody plants species have been around for a fraction of that time but have become established at an alarming rate. These exotic invaders have not evolved with the native ecosystems and therefore have developed no predators or diseases to keep their numbers in check. They are able to quickly invade and establish in fields, forests, and wetlands, assisted by animals and man (Webster et al., 2006; Lee and Thompson, 2012; Converse, 1984; Frappier et al., 2003a; Cygan, 2011; Jenkins and Parker, 2000). Many current invasive species were brought to the United States as horticulture plants or for erosion control (Reichard and White, 2001; Reichard, 1997). They have now spread to the forest and can inhibit the growth of native species by occupying growing space and competing for resources (Fagan and Peart, 2004; Dukes et al., 2009; Orr et al., 2005).

There are many direct control methods available to deal with nuisance vegetation. Chemical applications, mechanical pulling and cutting, bio-control, and management through cattle browsing are all reasonable options on a small scale (Luginbuhl et al., 1996; Cygan, 2011). However, these methods are expensive, time consuming, and not feasible in some circumstances. Once the invasive species has become well established in the forest, it not only costs money to remove it, but it inhibits tree growth and delays time until harvest. These invasive species are becoming more prominent with climate change as native species become more stressed in the changing environment (Dukes et al., 2009).

One of the most problematic invasive species in New England is glossy buckthorn (*Frangula alnus* Mill.). This species quickly establishes in a forest and, in some cases, can create a thick understory monoculture inhibiting growth and regeneration of native species (Webster et al., 2006; Fagan and Peart, 2004). It effectively changes the ecosystems it invades, creating dense shade and altering ground layer species (Fagan and Peart, 2004). There is even evidence that invasive species litter is preferred by some earth worms, affecting litter layer depth, composition, and soil properties such as nitrogen mineralization (Stokdyk and Herrman, 2014).

A primary concern for managers is how to naturally regenerate economically important native tree species without extreme effort and high cost. An important motivation for managing a forest involves harvesting timber to support a broad range of landowner goals and objectives including making money to invest in the forest. After a harvest, buckthorn can regenerate aggressively, quickly distributing across the site and growing faster than native species (Frappier et al., 2003a, 2004; Fagan and Peart, 2004). Buckthorn can outcompete the more economically important shade intolerant and mid tolerant tree species in the early stages of development, giving rise to a low value stand and longer rotation period. This problem is further exacerbated by browsing. Wildlife preferentially browse native vegetation over exotic invasive species, affecting sapling form and reducing native species numbers in an already stressed environment (Cappuccino and Carpenter, 2005; Culbreth and Hairston-Strang, 2011; Eschtruth and Battles, 2009).

To more effectively combat glossy buckthorn managers need more information. They need knowledge of what environmental factors are associated with its distribution so they can understand why it occurs in certain areas versus others. There is a broad understanding as to where woody invasive species grow as a whole. They are primarily found on disturbed sites, forest edges, along roads, and in forests that were historically fields (Lee and Thompson, 2012; Burnham and Lee, 2010; Lundgren et al., 2004; Olson et al., 2011; Koning and Singleton, 2013; Johnson et al., 2006; Cunard and Lee, 2009; Evans et al., 2006). Glossy buckthorn is a frequent inhabitant in white pine (*Pinus strobus* L.) forests (Fagan and Peart, 2004; Frappier et al., 2003a,b; Cunard and Lee, 2009; Burnham and Lee, 2010; Lee and Thompson, 2012). There is a lack of specific knowledge as to where buckthorn grows. Olson et al. (2011) were unable to attribute buckthorn growth to any of the environmental variables they measured in the Penobscot Experimental Forest, Maine. Others have found that glossy buckthorn is an inhabitant under white pine but decreases in density as basal area increases, specifically the basal area of shade tolerant trees (Cunard and Lee, 2009; Koning and Singleton, 2013).

The objective of this research was to gain a more in-depth understanding of what environmental factors are associated with glossy buckthorn density and how it affects regeneration. We sampled numerous sites across New Hampshire that have a buckthorn component in the forest (**Figure 1, Appendix A, B**). At each site, environmental variables thought to be related to buckthorn density were measured and compared across sites with different levels of invasion. The aim was to understand why buckthorn grew where it was as opposed to an area adjacent to a thicket where there were few to no stems. This information was used to create a prescription risk tree to aid foresters who may be uncertain how to proceed in their management with the threat of buckthorn invasion. With this information, forest managers will be better able to control buckthorn and the risk it poses to native regeneration without the need for intense direct control and expense.

Thesis Organization

The balance of the thesis consists of two chapters addressing glossy buckthorn. Chapter II is written as a manuscript intended for submission to an appropriate journal, therefore, it is largely independent and stands on its own. It reviews research conducted over two years identifying environmental factors associated with buckthorn densities and recommendations for indirect management in the face of risk of buckthorn invasion in a forest. A thorough review of current literature was conducted to identify gaps in knowledge of glossy buckthorn. Three forested locations across New Hampshire were sampled and the data were analyzed to find associations between glossy buckthorn density and environmental variables. These data also included information about the effect of buckthorn on native tree regeneration. This information was organized into a prescription risk tree to assist forest managers in their prescriptions in the face of buckthorn.

Chapter III acts as a conclusion, summarizing the results of the previous chapter and discussing implications for forest management. Finally we discuss limitations of our study and suggest areas that need further research to gain a more complete understanding of glossy buckthorn in New England.

CHAPTER II

ENVIRONMENTAL VARIABLES ASSOCIATED WITH INVASIVE GLOSSY BUCKTHORN (*FRANGULA ALNUS* MILL.) AND INDIRECT CONTROL STRATEGIES FOR FOREST MANAGERS

Abstract

Glossy buckthorn (*Frangula alnus* Mill.) is one of the most prominent nonnative invasive woody plant species affecting New England forests. We investigated the environmental variables associated with glossy buckthorn density and its effect on native tree regeneration in forested ecosystems by sampling in three locations across New Hampshire, USA. The objective was to gain an understanding of where glossy buckthorn grows to better manage the species indirectly through silviculture and management. Glossy buckthorn was found at its highest densities in disturbed white pine (*Pinus strobus* L.) forests that were historically old fields, with a thin organic layer and low herbaceous cover, on drained loam and clay soils. Scatter plots and generalized linear models showed that organic layer thickness, dominant overstory species, percent herbaceous cover, drainage class, soil type, historical land use, and evidence of harvest were the most influential variables in predicting density of buckthorn. Relationships between buckthorn and environmental variables were much stronger in softwood stands than hardwood stands. Softwood stands were primarily composed of white pine and some eastern hemlock (*Tsuga canadensis*). We found evidence of direct competition between glossy buckthorn and native regeneration although there was no effect on the average shade tolerance of native species regenerating with glossy buckthorn present. With this information we designed a proto-type prescription risk tree for forest managers faced with risk and uncertainty when planning a harvest in the presence of glossy buckthorn.

1. Introduction

Researchers and practitioners have long recognized the ecological threats posed by invasive plant species to forests. Dukes et al. (2009) cited several studies indicating that invasive species hinder regeneration of native forest tree species, especially in younger, physically disturbed forests. Invasive plants quickly establish and flourish and can form a dense monoculture in the forest understory altering ground level species composition and abundance, effectively outcompeting the native understory (Lee and Thompson, 2012; Converse, 1984; Frappier et al., 2003a; Webster et al., 2006; Cygan, 2011; Orr et al., 2005). Intense competition in the forest understory from an invasive species means reduced canopy recruitment and a change in forest properties (Frappier et al., 2003a; Dukes et al., 2009). Wildlife may prefer native vegetation over nonnative invasive species as browse, further increasing pressure on tree regeneration (Cappuccino and Carpenter, 2005; Culbreth and Hairston-Strang, 2011). Invasive species are the second most important threat to biodiversity behind habitat loss and degradation (Wear and Greis, 2002).

Among the many non-native invasive plant species, glossy buckthorn (*Frangula anlus* Mill., hereafter referred to as buckthorn) has been an especially troublesome invasive in New England. New England consists of 6 states in northeastern USA; Maine, New Hampshire, Vermont, Massachusetts, Connecticut, and Rhode Island. Fagan and Peart (2004) indicate buckthorn inhibits tree recruitment and regeneration, thereby favoring the regeneration of shade tolerant tree species. Many of the most valuable tree species in New England, including white pine (*Pinus strobus* L.) are moderate to shade intolerant, and the loss of these species (or substantial delays in their recruitment and growth) can have a significant negative impact on the financial return to forest owners. The decline in timber value increases the pressure to convert to developed land uses, therefore exacerbating the loss of forest cover and biodiversity. Dukes et al. (2009) predicts that with climate change, buckthorn will be an increasing problem to forests.

Managers play a very influential role in regeneration success in areas prone to invasive species. However, foresters often question how to address nonnative plant invasion in their silvicultural prescriptions, unsure of the risks associated with invasion and the impacts on successful native tree regeneration. Burnham and Lee (2010) found that buckthorn was 96 times more abundant in logged areas than in undisturbed sites. Scarification to mineral soil associated with harvests appears to assist invasion (Lee and Thompson, 2012; Olson et al., 2011). Cunard and Lee (2009) found buckthorn is less abundant as basal area of shade tolerant tree species increases, as photosynthetically active radiation decreases, and as soil nutrients decrease. They infer that buckthorn will eventually be outcompeted by shade tolerant tree species.

Olson et al. (2011) investigated invasive plants in the Penobscot Experimental Forest in Maine, USA with the objective of relating their abundance and distribution to management history and environmental factors. They found ten invasive plant species, primarily in forests originating from old fields and fewer species in the silviculture experiment area which had never been cleared for agriculture but had been repeatedly cut (Olson et al., 2011). In old field sites invasive species were positively related to exposed mineral soil and negatively related to hardwood litter cover and soil organic layer depth (Olson et al., 2011). Buckthorn was the most common invasive species in both the old field and forest sites, however, they were unable to relate its density to any of their observed factors. There is a broad understanding that buckthorn is associated with recently harvested areas, forests that have grown from old fields, and under white pine (Lee and Thompson, 2012; Burnham and Lee, 2010; Lundgren et al., 2004; Olson et al., 2011; Koning and Singleton, 2013; Johnson et al., 2006).

The focus of this study was to expand our understanding of environmental factors associated with buckthorn establishment and how it can affect native tree regeneration in the hopes of assisting foresters with management decisions in the face of risk and uncertainty, while expanding our knowledge of buckthorn. It is impossible to completely eradicate nonnative invasive plants from our forests without intense effort and cost (Lee et al., in prep). In areas of extreme invasion, direct control may no longer be a viable method, indirect control through forest management practices may be the only option. An important output of the study is a prescription risk tree to aid forest managers. Using this prescription risk tree, forest managers will be better able to tailor their treatments to hopefully reduce the risk of invasion or reduce the invasion's impact on desirable native tree regeneration.

2. Methods

2.1 Study area

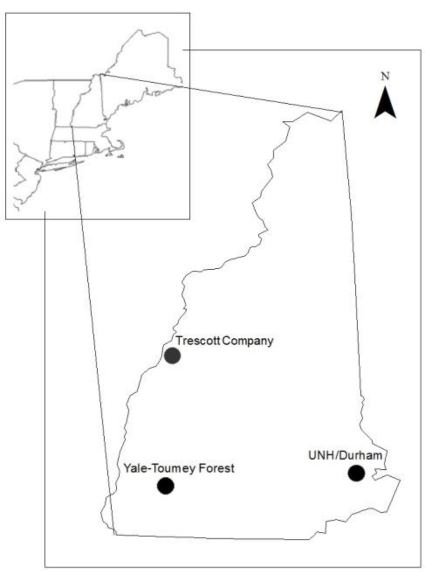


Figure 1. Sampling locations across New Hampshire

The data for this study were collected in three locations across New Hampshire, USA (Fig. 1). Sites were selected for their proximity to buckthorn populations, intensity of forest management for timber and ecosystem quality, and availability of management records. Sampling focused on naturally regenerated stands. No stands were 'virgin' forest; all have undergone some form of anthropogenic disturbance since the time of European settlement. Eleven properties were sampled in the first location, Durham, NH, where buckthorn is well established (Frappier et al., 2003a; Cunard and Lee, 2009; Burnham and Lee, 2010). Eight of those properties are owned by the University of New Hampshire (UNH) and actively managed for timber, wildlife, and recreation. Two of the other properties, the Oyster River Forest and Doe Farm, are owned by the Town of Durham, and the last, The Lamprey River Preserve, is owned and managed by The Nature Conservancy.

The second location is land owned by the Trescott Company in Hanover, NH. It was chosen for its high variability in buckthorn density and intense management. This land is a mixture of plantation and natural stands of softwood and hardwood forest types at different elevations and aspects. It is the municipal water source for the town of Hanover.

The last location is the Yale-Toumey Forest in Swanzey and Keene, NH, owned and managed by Yale University. The Yale-Toumey forest is a working research forest with a long history of management for white pine.

2.2 Sampling

Sampling was conducted in transects running from areas of little to no buckthorn through areas of high buckthorn density to identify the variables that may be controlling those densities. Nested plots were used at each point to identify overstory composition, understory composition, and general site characteristics. A basal area factor 20 ft^2/ac prism was used to select sample trees to measure. Species and diameter at breast height (dbh) was recorded for each sample tree greater than or equal to 3 inches in diameter. These trees were used to determine tree species composition and basal area. Using the same center point, a 5ft radius circular plot was established. Within this plot, all tree species less than 3 inches were counted, identified, and measured by height class: 0-2ft, 2-4ft, 4-8ft, 8-12ft, 12+ft. All buckthorn stems within these plots were also counted and measured by height classes comparable to those of the tree regeneration. In these plots, visual estimates of hardwood to softwood litter cover ratio, percent exposed mineral soil, and herbaceous cover were made. Canopy cover was calculated by taking a picture skyward above plot center at dbh and uploading the image to an automatic thresholding algorithm (Nobis and Hunziker, 2005) in MATLAB (2015) adapted by Ducey (2016). This code detects the edge of canopy and sky and calculates the gap fraction of each. A small hand trowel was used to take a soil sample at each plot from the upper B horizon to determine organic layer thickness and identify the soil as sand, loam, clay, or a combination of two of those by hand texturing. Evidence of previous harvest was categorized by the presence/absence of sawn stumps in any decay stage. Drainage class was classified as wet, somewhat drained, drained, and well drained depending on vegetation, soil type, presence of water, and decomposition state of the duff. Historical land use was determined by records, personal communication, and visual evidence (stone walls, plow windrows, barbed wire, etc.). These variables were thought to be the most probable drivers of buckthorn densities and can also be quickly and easily measured by forest managers.

Based on the literature we expected there would be a relationship between buckthorn and these variables: land use history, dominant overstory species, percent canopy cover, evidence of harvest, organic layer thickness, soil drainage class, soil type, and percent exposed mineral soil. It was hypothesized that forests originating from old fields would support more buckthorn than forests that have historically been forests (Fagan and Peart, 2004; Lee and Thompson, 2012; Olson et al., 2011; Koning and Singleton, 2013; Johnson et al., 2006). Many studies have found that buckthorn is positively associated with an increase in white pine basal area (Fagan and Peart, 2004; Frappier et al., 2003a,b; Cunard and Lee, 2009; Burnham and Lee, 2010; Lee and Thompson, 2012). It has been found that buckthorn density increases as canopy cover reduces

(Koning and Singleton, 2013; Cunard and Lee, 2009; Lee and Thompson, 2012). Williams and Krock (2012) found that buckthorn density is greatest on drained soils, while Lundgren et al. (2004) found that loam and clay soils support greater densities of buckthorn than coarse, sandy soils. Buckthorn is usually associated with disturbance in the form of harvest and scarification to mineral soil (Burnham and Lee, 2010; Olson et al., 2011). Olson et al. (2011) provides evidence that invasive species are more commonly found on thin organic layers and less common on soils with thick organic layers.

2.3 Buckthorn analysis

To examine how buckthorn is associated with the different environmental variables sampled we used the number of buckthorn stems per plot, or density, and relative spacing (RS) of those stems to compare against environmental variables and regeneration data. JMP Pro 12 was used in all analyses unless noted. The number of buckthorn stems in a plot and their heights were applied to an equation to calculate the relative spacing of buckthorn at that plot. To create the relative spacing measure we used weighted sum of squared heights to infer density and create the quadratic relative spacing equation used on all sample plots. This was based on Chisman and Shumacher (1940) where sample plot data was used to develop a tree-area ratio according to dbh of individual trees by means of a quadratic equation fitted by least squares for uneven-aged stands. Their equation was set to 1, the maximum, and regression was used to estimate the unknown parameters of the maximum density equations using tree diameter as the size of the tree. This approach has been expanded to mixed species stands using dbh and putting individual species into groups to lessen the number of parameter estimates (Stout and Nyland, 1986; Stout et al., 1987). Ducey and Knapp (2010) used specific gravity of the wood to create an equation to estimate relative density that accommodates a wide range of species compositions and diameter distributions. The idea of using height instead of diameter was introduced by both Hart (1928) and Wilson (1946). Ducey and Kershaw (2011) detail how it is possible to use a height squared factor in place of the more commonly used basal area factor associated with angle gauges to determine forest measurements.

These ideas were used to create a relative spacing formula for the forest understory. The equation assumes an uneven-aged stand (buckthorn) that happens to have an overstory above it. Height of each stem was used as opposed to dbh because of the small diameter variation and therefore height is a better predictor of the make-up of the understory. To formulate the quadratic equation, 12 plots were identified as having the highest density of buckthorn by examining buckthorn stem count data and analyzing plot pictures. These 12 plots were used to calculate coefficients for the equation through standard least squares assuming an intercept, or maximum, of 1. This equation (Equation 1) was applied to all plots. The relative spacing values ranged from 0-1, no stocking to fully stocked, with some values over 1 meaning they were overstocked.

Standard errors were calculated using R (R Core Team, 2015). The coefficients were not well constrained. The formula was not meant to choose the best model; dropping some variables did not significantly improve standard errors or Akaike information criterion (AIC) values (Burnham and Anderson, 2002) (Table 1). The objective of creating a relative spacing measure for the understory was meant to follow Chisman and Shumacher (1940). Predictions of relative spacing values had a similar distribution to plot stem counts.

$$\max\left(aN + b\sum H + c\sum H^2\right) = 1$$

Equation 1. Relative spacing formula created based on number of buckthorn stems and their heights. The same equation with different coefficients was used for regeneration relative spacing. *N*= number of stems, *H*= height of the stems, *a,b,c*= coefficients (midpoint of height class- 1ft, 3ft, 6ft, 10ft, 13ft).

Scatter plots were used to compare levels of buckthorn density and relative spacing against individual variables. Scatter plot points are stem counts at individual sample points. The scatter plots served as initial analysis to choose which variables may be the most associated with buckthorn density. These variables were run in many different combinations in a generalized linear model using a Poisson distribution. Many combinations were run, including and excluding each variables until the lowest AIC value was obtained. The Poisson distribution was a better fit for the distribution of plot stem counts than a Normal distribution; there were a large number of low counts with fewer large counts. The parameter estimates calculated by the generalized linear model were examined to further determine which variables were most associated with buckthorn density. A positive parameter estimate means buckthorn density is associated with the variable, a negative value means buckthorn density is negatively associated with that variable. Overstory composition was analyzed by major species and separated into softwood (primarily white pine) or hardwood. Analyses were repeated on the hardwood and softwood sites separately for the possibility of different relationships.

2.4 Regeneration analysis

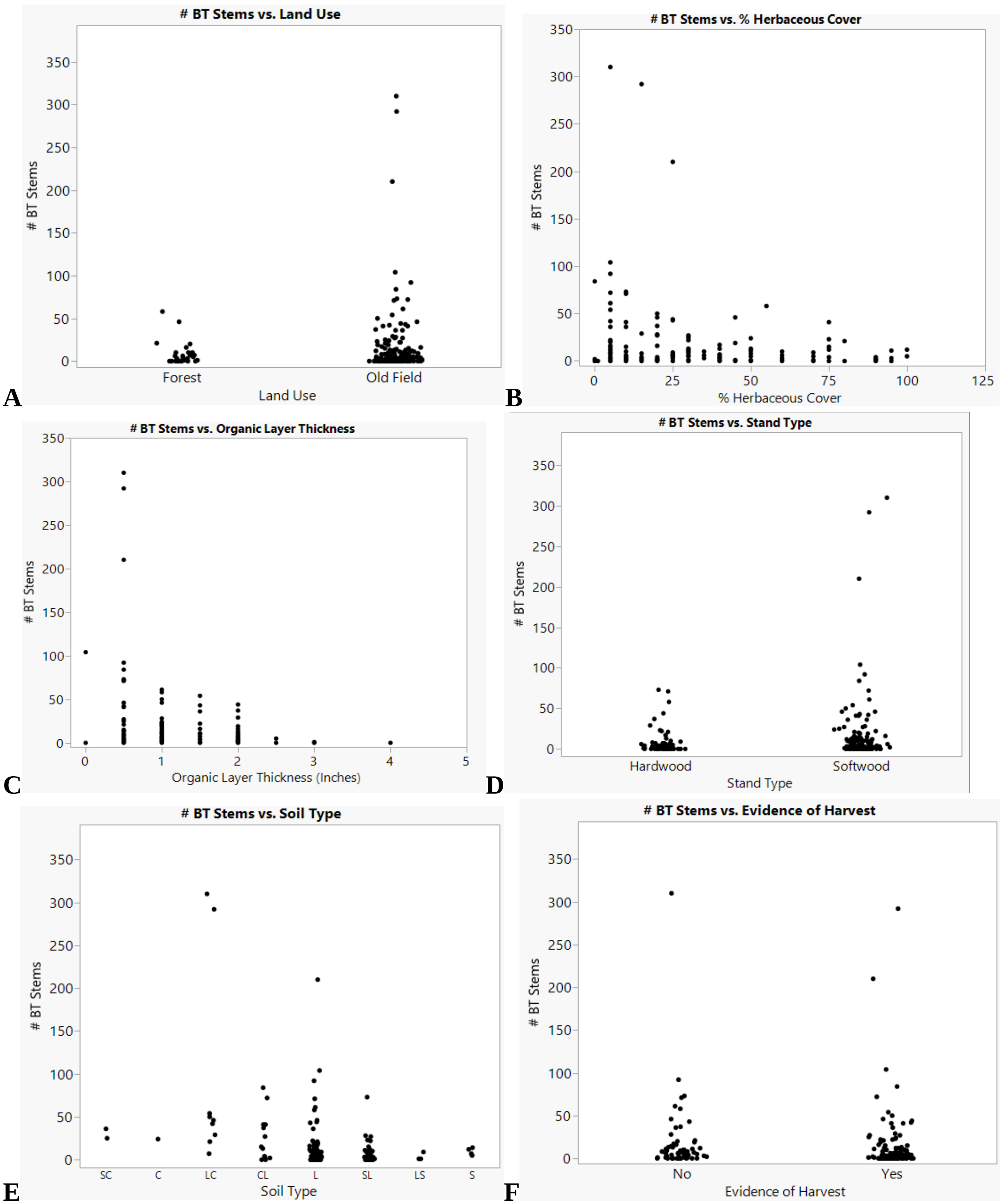
Data for native forest tree sapling and seedling stems were analyzed similarly to the buckthorn data. A relative spacing value based on the number of stems and their heights (Equation 1) was calculated for each plot. The coefficients used in the relative spacing formula were based on 10 plots with the highest regeneration stem counts. The relative spacing values for native trees were compared with the buckthorn relative spacing values, along with the stem counts per plot. To examine how shade tolerance of regeneration may be affected by buckthorn density and relative spacing, each regenerating species was assigned a shade tolerance value given by Niinemets and Valladares (2006) on a scale of 0 (minimum tolerance) to 5 (maximum tolerance). Shade tolerance values were averaged for each plot and graphed against buckthorn stem count and relative spacing.

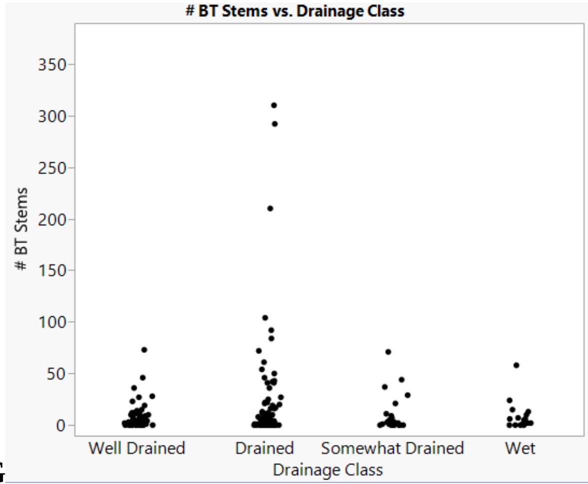
3. Results

3.1 Buckthorn analysis

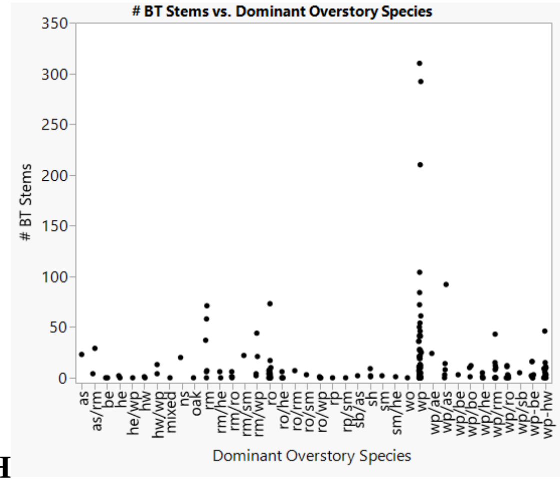
Buckthorn relative spacing ranged from 0.00 to 1.65. Stem counts of buckthorn ranged from 0 to 310 in the 5ft radius plots. In the 55 plots located in pure white pine stands there were a total of 1,807 buckthorn stems; in the 143 other plots, including those with a white pine component, there were 1,023 stems. Sixty-five percent of the buckthorn stems measured were under 2ft in height. Softwood plots averaged 17.6 buckthorn stems while hardwood plots averaged 7.9 stems.

There were some obvious trends found between the number of buckthorn stems and environmental variables. Forests originating from old fields had a greater abundance of buckthorn than forests that have historically been forests (Fig. 2A). As herbaceous cover increased, buckthorn density decreased (Fig. 2B). Organic layer thickness of the soil shows a strong negative relationship to buckthorn density (Fig. 2C). Buckthorn density was higher in softwood stands than hardwood stands (Fig. 2D). Buckthorn was most often associated with loamy soils and soils with a mixture of loam and clay; it was least associated with sandy soils (Fig. 2E). There was a weak difference in buckthorn density between sites that had evidence of harvesting or not (Fig. 2F). Buckthorn was most associated with drained soils (Fig. 2G). The highest density of buckthorn stems were found in white pine dominated stands (Fig 2H). Buckthorn seemed to be found in areas with small amounts of exposed mineral soil (Fig 2I). Buckthorn density does not appear to be related to basal area of the overstory (Fig. 3A). There seems to be no relationship between number of buckthorn stems and canopy cover (Fig. 3B). The hardwood to softwood litter ratio was plotted as the percent hardwood litter, which shows no relationship to the number of buckthorn stems (Fig. 3C).

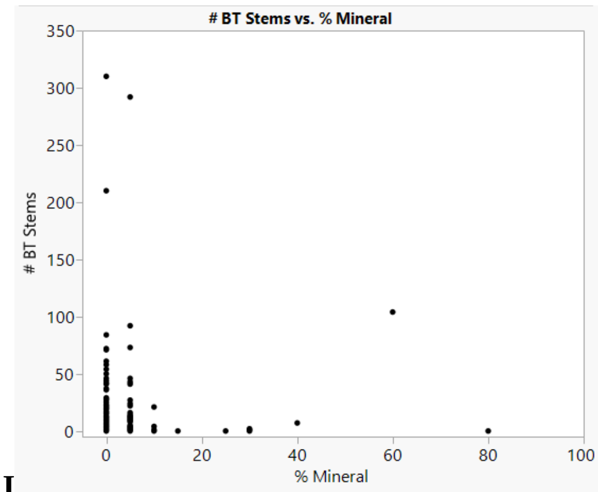




G



H



I

Figure 2. Scatter plots comparing number of buckthorn stems to select environmental variables that show a trend. (E) SC= sandy clay, C= clay, LC= loamy clay, CL= clay loam, L= loam, SL= sandy loam, LS= loamy sand, S= sand.

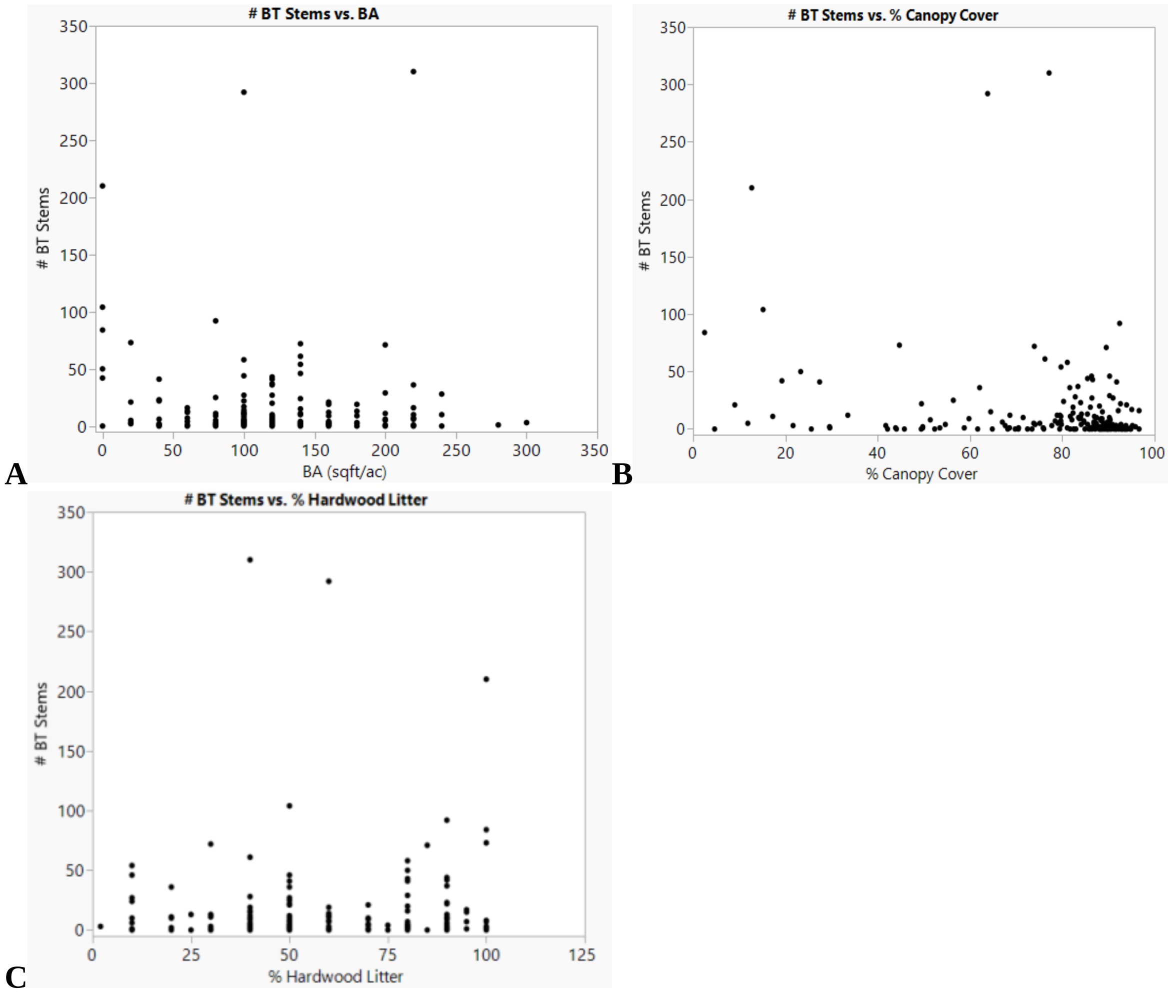


Figure 3. Scatter plots comparing number of buckthorn stems to environmental variables that show no trend.

When analyzing the variables associated with buckthorn density separately between hardwood and softwood, some relationships changed from that observed for the aggregate of forest types. Overall relationships were stronger in the softwood stands; buckthorn densities in the hardwood stands were weakly associated with the same variables, if at all. The biggest difference between softwood and hardwood stands was in organic layer thickness (Fig. 4A, 4B). In softwoods stands there was a strong inverse relationship between organic layer thickness and buckthorn stem counts (Fig. 4A), in hardwood stands this changed to a weak positive relationship (Fig. 4B). In softwood stands there is a clear association with drained soils and buckthorn density (Fig. 4C). In the hardwood stands the association is less clear as to which type of drainage class buckthorn has higher densities in (Fig. 4D).

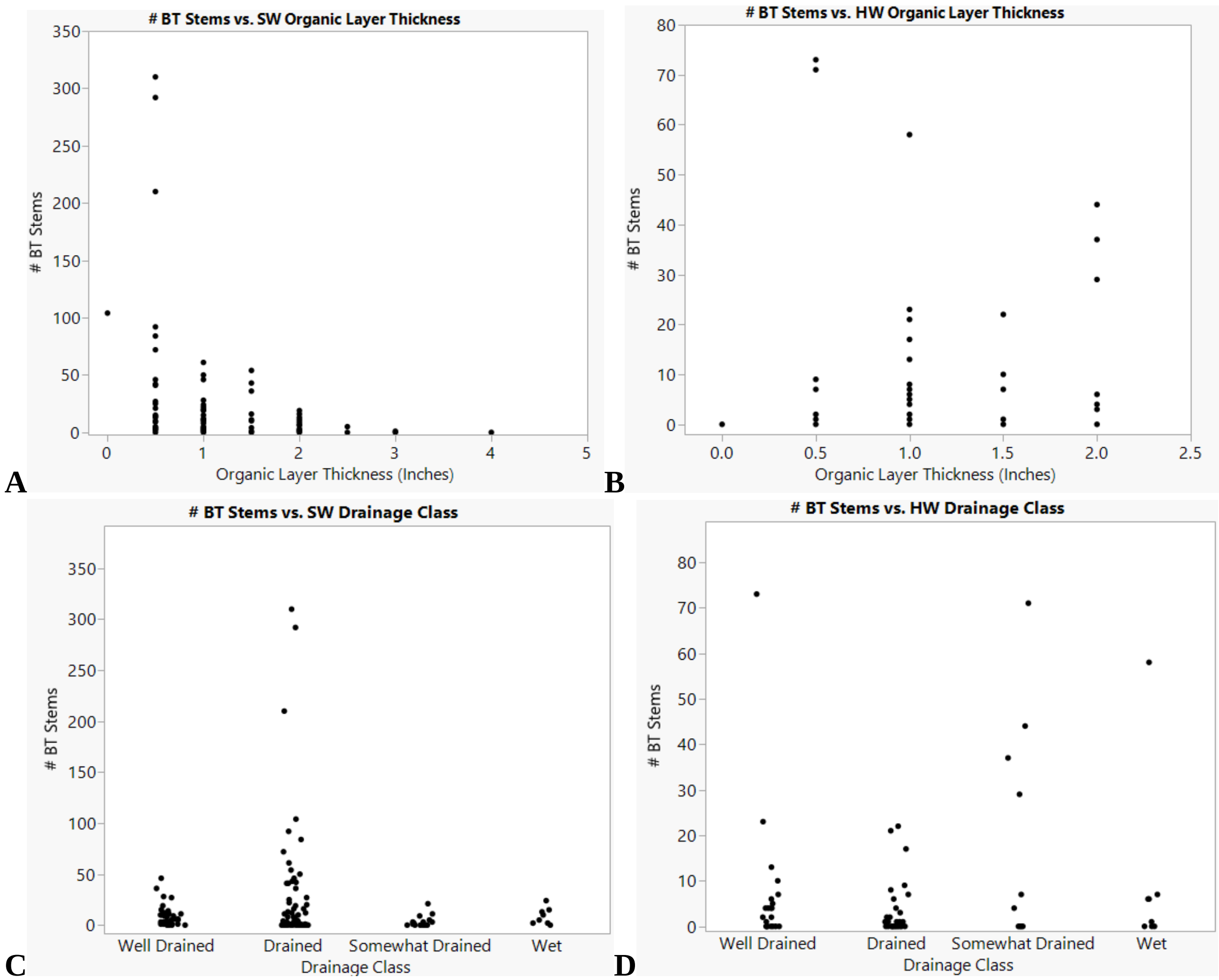


Figure 4. Scatter plots comparing softwood (SW) and hardwood (HW) stands. These variables were the most influenced when separating stand type. Organic layer thickness (top) is inverse between stands types. A strong relationship is shown between drainage class (bottom) in softwood stands (C) while a weak relationship is shown in hardwood stands (D).

The set of variables with the lowest AIC value (3,231.82) were: organic layer thickness, overstory species, percent herbaceous cover, drainage class, soil type, land use, and evidence of harvest (Table 2). These variables are statistically the most strongly associated with buckthorn stems counts. Table 2 shows a range of poor to best model combinations. Multiple combinations were tested with all variables considered until the best mode, with the lowest AIC value, was obtained. Parameter estimates calculated with the generalized linear model show that soil type had both the highest and lowest magnitude (Table 3). Replacing stand type (hardwood or softwood) with dominant overstory species lowered the AIC value by over 2,000 (Table 2). The effect of overstory composition is shown by parameter estimates (Table 4). The species that were most often associated with buckthorn are white pine and red maple (*Acer rubrum*) with lesser amounts associated with red oak (*Quercus rubra*) (Table 4). Species associated with the least amount of buckthorn were eastern hemlock and mixed hardwoods (Table 4). Forests dominated by white pine have a high parameter estimate (4.66), unless there is a beech (*Fagus grandifolia*) or hemlock component in the understory (2.29, 1.03) (Table 4). The variables changed when separating softwood and hardwood stands and the relationship became more complex. In softwoods stands, the variables with the lowest AIC (2,445.83) were soil type, organic layer thickness, drainage class, land use history, evidence of harvest, and canopy cover; parameter estimated are given in table 5A. In hardwood stands, the variables with the lowest AIC value (681.94) was with soil type, percent herbaceous cover, evidence of harvest, drainage class, canopy cover, land use history and basal area; parameter estimates are given in table 5B.

Table 1. Coefficient values and standard errors for the relative spacing equation for both buckthorn and regeneration.

Buckthorn			Regeneration		
Coefficient	Value	Standard Error	Coefficient	Value	Standard Error
a	0.000749	0.010068	*a*	0.250523	0.023196
b	0.004469	0.009631	*b*	-0.015804	0.021705
c	-0.000428	0.001057	*c*	0.0012714	0.001815

Table 2. Generalized linear model AIC outputs with number of buckthorn stems as the dependent variable. Select combinations of environmental variables are included in the table. The lowest AIC value shows the variables most associated with buckthorn density. Variables were included in the model if there was a trend shown in the scatter plot.

Variable	**AIC**
O Thickness, Overstory Species, % Herbaceous Cover, Drainage Class, Soil Type, Land Use, Evidence of Harvest	3,231.82
O Thickness, Overstory Species, % Herbaceous Cover, Drainage Class, Soil Type, Land Use	3,366.54
O Thickness, Overstory Species, % Herbaceous Cover, Drainage Class, Soil Type	3,540.22
O Thickness, Overstory Species, % Herbaceous Cover, Drainage Class	3,815.89
O Thickness, Stand Type, % Herbaceous Cover, Drainage Class, Overstory Species	4,053.42
O Thickness, Stand Type, % Herbaceous Cover, Drainage Class	5,828.32
O Thickness, Stand Type, % Herbaceous Cover, Land Use	6,018.31
O Thickness, Harvest, Land Use, Stand Type	6,133.74
O Thickness, Stand Type, Land Use	6,345.52
Herbaceous Cover, Land Use, % Mineral Soil	7,656.31

Table 3. Parameter estimates for all variables other than dominant overstory species for the best generalized linear model.

Variable	Parameter Estimate
Soil Type: Loamy Clay	18.7580
Soil Type: Loam	17.7064
Soil Type: Sandy Clay	17.6088
Soil Type: Clay Loam	17.5631
Soil Type: Sand	17.4392
Soil Type: Loamy Sand	16.9188
Drainage Class: Drained	0.5162
Harvest: No	0.2890
% Herbaceous Cover	-0.0056
Drainage Class: Somewhat Drained	-0.0063
Drainage Class: Wet	-0.4483
Land Use: Forest	-0.6252
Organic Layer Thickness	-0.9864
Soil Type: Clay	-123.0702

Table 4. Parameter estimates calculated using a generalized linear model with Poisson distribution. Positive numbers are more associated with increased buckthorn density while negative numbers are more associated with decreased buckthorn density. (A) Overstory species compositions represented in five or more plots. (B) All stands with a white pine component. Dominant overstory species names organized by most dominant/second most dominant.

A. Dominant Overstory Species	Parameter Estimate
white pine	4.66
red maple	4.58
white pine/aspen[1]	4.34
white pine/red maple	3.20
red oak	3.10
white pine/red oak	2.29
white pine/hemlock	1.03
hardwood mix	-0.42

B. Dominant Overstory Species	Parameter Estimate
white pine	4.66
white pine/elm[2]	4.36
white pine/aspen	4.34
red maple/white pine	4.06
hardwood mix/white pine	3.33
white pine/black oak	3.22
white pine/red maple	3.20
white pine/black birch[3]	2.80
white pine w/ beech understory	2.77
white pine/beech	2.29
white pine/red oak	2.29
white pine/hemlock	1.03
red oak/white pine	0.09
hemlock/white pine	-12.15

[1] *Populus tremuloides* [2] *Ulmus americana* [3] *Betula lenta*

Table 5. (A) Parameter estimates for the best generalized linear model analyzing only hardwood stand types. (B) Parameter estimate for the best generalized linear model analyzing only softwood stand types.

A. Variable	Parameter Estimate
Drainage Class: Somewhat Drained	1.9358
Harvest: No	1.1444
Soil Type: Loamy Clay	0.5909
Soil Type: Sand	0.4826
Drainage Class: Wet	0.0377
% Herbaceous Cover	0.0220
Basal Area	-0.0076
Canopy Cover	-0.0189
Soil Type: Loam	-0.3058
Land Use: Forest	-0.5397
Drainage Class: Drained	-0.8747
Soil Type: Clay Loam	-1.5302

B. Variable	Parameter Estimate
Soil Type: Clay	1.6570
Soil Type: Loamy Clay	1.2191
Drainage Class: Drained	0.8277
Harvest: No	0.3804
Soil Type: Sandy Clay	0.1020
Canopy Cover	-0.0081
Soil Type: Loam	-0.1108
Soil Type: Clay Loam	-0.1151
Drainage Class: Somewhat Drained	-0.4929
Drainage Class: Wet	-0.6056
Land Use: Forest	-0.6626
Soil Type: Loamy Sand	-0.7343
Soil Type: Sandy Clay	-0.9389
Organic Layer Thickness	-1.2249

3.2 Regeneration analysis

There was an average of 17.9 native seedlings and saplings per plot with a dbh less than 3in. On plots where buckthorn was present, there was an average of 21.11 buckthorn stems and 19.65 native seedlings and saplings. The graph of the relationship between regeneration shade tolerance and buckthorn relative spacing is rather flat suggesting they are not related (Fig. 5A). Glossy buckthorn has a shade tolerance of 2.66 (Niinemets and Valladares, 2006). Figure 5B shows the relationship between regeneration relative spacing and buckthorn relative spacing. Figure 5B is a triangular shape, even if extreme values are removed. This triangular shape means there is an inverse relationship between buckthorn relative density and tree regeneration. The hypotenuse of the triangle is approximately a 45 degree angle, suggesting direct competition between buckthorn and tree regeneration (Fig. 5B). Although not shown, when comparing the number of regenerating stems to the number of buckthorn stems the shape is similar to Figure 5B.

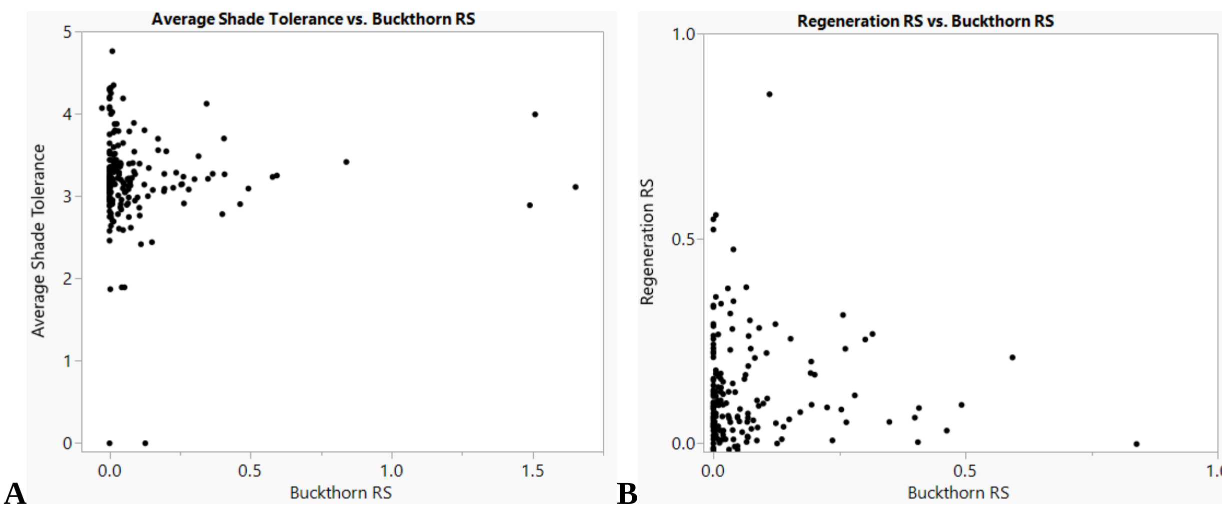


Figure 5. (A) The average shade tolerance of the regeneration compared to buckthorn relative spacing. (B) The relative spacing of regeneration versus the relative spacing of buckthorn.

4. Discussion

4.1 Buckthorn analysis

To manage nonnative invasive species resource managers need to understand their ecology and how they interact with native vegetation. Glossy buckthorn distribution in forests is clearly associated with several of the variables sampled. Our results were consistent with much of the literature, although there were some disagreements. Buckthorn is most commonly found in disturbed (evidence of harvest, exposed mineral soil) softwood forests, primarily white pine (Fig. 2D, 2F, 2H, 2I). This is consistent with much of the literature (Lee and Thompson, 2012; Catling and Porebski, 1994; Johnson et al., 2006; Fagan and Peart, 2004; Cunard and Lee, 2009; Burnham and Lee, 2010). Also expected, buckthorn was found in old field sites (Fig. 2A), in association with thin organic layers (Fig. 2C), low herbaceous cover (Fig. 2B), on loamy and clayey soils (Fig. 2E), and on drained soils (Fig. 2G). There was a very clear relationship between organic layer thickness and buckthorn density. A thick organic layer could reduce the ability of buckthorn to establish, or the decreased organic layer could be a product of the presence of buckthorn. Knight et al. (2007) found that common buckthorn (*Rhamnus cathartica*) was the preferred food for invasive European earthworms, which increased litter decomposition, decreasing organic layer thickness.

We found that buckthorn density was not associated with canopy cover and basal area (Fig. 3A, 3B). Buckthorn was in very open areas and under dense, closed canopies. Lee and Thompson (2012) found that buckthorn can readily invade and regenerate under closed canopies of white pine. Basal area as a whole was not important, but as the ratio of softwood species increased, there was an increase in buckthorn (Fig. 2D).

Combinations of these variables seem to provide the best habitat for buckthorn. In an ecosystem, all of these different variables interact, influencing what species can establish, how much light there is, nitrogen availability from the soil, and other variables. This makes it hard to say with complete certainty that one variable is the primary catalyst for buckthorn invasion. The combination of different variables leads to an environment where buckthorn is capable of establishing. Changing one variable, such as establishing herbs on the forest floor, may not itself reduce the amount of buckthorn. The low herbaceous cover may be a result of something else such as the dominant overstory species, the past land use, the organic layer thickness, or the shading effect of buckthorn.

Ecosystems are a complex web of interactions and buckthorn grows on many sites. The presence of buckthorn in white pine stands may not be related to the white pine directly but indirectly by the wildlife habitat it provides, for example. White pine provides foraging and roosting habitat for many mammal and bird species (Yamasaki, 2003). Roosting birds introduce high concentrations of seeds, including buckthorn seeds, in their droppings to the forest floor. It is impossible to keep birds out of a forest, but managers can influence some of the variables associated with high buckthorn density through management.

During sampling it was observed that most of the buckthorn occurred in thickets surrounded by dissipating densities. The Yale-Toumey Forest was in an area of overall low buckthorn invasion, unlike the UNH/Durham area and Trescott Company watershed. At the Yale-Toumey Forest buckthorn was not clumped but spread evenly at low densities throughout the property. At properties with high densities, most interesting was when buckthorn population boundaries followed a straight line through the forest. In areas of recent disturbance creating canopy gaps there was a clear increase in buckthorn density.

According to the generalized linear model, the most influential variables were organic layer thickness, dominant overstory species, percent herbaceous cover, drainage class, soil type, land use history, and evidence of harvest (Table 2). These variables can quickly and easily be identified by a forester or land manager. If there is a thin organic layer with low herbaceous cover on loam or clay drained soils in an old field softwood forest, there is a high probability of the invasion of buckthorn if one were to harvest. These important variables change when analyzing hardwood and softwood sites separately in the generalized linear model and the scatter graphs. When analyzing the scatter graphs the relationships are much stronger in softwood forests while in hardwood forests density seems more scattered among the variables (Fig. 4C, 4D). The relationship between organic layer thickness is opposite in softwood and hardwood sites (Fig. 4A, 4B). This was the most dramatic difference between the two forest types. This suggests that it is easier to influence buckthorn densities in softwood sites through management because of those stronger relationships. In hardwood sites there is less of a chance of having high densities of buckthorn but it is harder to control through management.

4.2 Regeneration analysis

We were able to find evidence of direct competition between native regeneration and buckthorn (Fig. 5B). Frappier et al. (2004) and Fagan and Peart (2004) found that buckthorn inhibits tree regeneration. By contrast there was no evidence of a change in shade tolerance of regeneration in the presence of buckthorn (Fig. 5A). Fagan and Peart (2004) measured saplings 4.26-16.40ft (1.3-5m) in height and found that in the presence of buckthorn, tree recruitment favored shade tolerance species, contrary to our findings. In our study we counted each regenerating stem, seedlings and saplings, up to 3in dbh. This includes a much greater range of regeneration ages. The shade tolerance values are on a scale of 1-5 (Niinemets and Valladares,

2006) so individual values will not dramatically affect the average shade tolerance, especially with so many stems present in each plot. Regeneration in a forest reflects events that happened years ago when the seeds established. The seeds could have established before buckthorn was in the environment and only the regeneration overtopped by buckthorn are being affected now. The regeneration could be based on a specific event such as a harvest, fire, or weather that favored that species. Seeds can easily germinate but the success of that seedling depends entirely on the environment around it. Cunard and Lee (2009) predict that buckthorn will be outcompeted in late successional stands due to its shade intolerance; this is consistent with its tolerance value of 2.66, similar to black oak (*Quercus velutina*), black cherry (*Prunus virginiana*), black birch, lilac (*Syringa vulgaris*), and red raspberry (*Rubus idaeus*) (Niinemets and Valladares, 2006). Buckthorn primarily germinates from seed although lateral vegetative (clonal) spread is possible (Lee and Thompson, 2012)

The lack of change in shade tolerance within the regeneration graph allows us to use regeneration as its own community group and compare its relative spacing against the buckthorn relative spacing (Fig. 5A, 5B). Regeneration relative spacing and average shade tolerance are not related. Figure 5B shows direct competition between buckthorn and regeneration. When the relative spacing of buckthorn nears 1, regeneration relative spacing nears 0. This relationship is nearly a 45 degree angle, even if removing the extreme values, suggesting that buckthorn and tree regeneration use the same resources. This direct competition is an important factor to consider in management. In the presence of buckthorn, any tree regeneration will have an even lower probability of survival given the already intense competition it faces. This could also be said in the reverse; in the presence of thick tree regeneration, buckthorn has a lower probability of survival. Anything one can do to promote native regeneration should reduce buckthorn abundance. The competition with buckthorn is further exacerbated by browsing. Animals preferentially browse native vegetation, increasing exotic invasive plant abundance (Cappuccino and Carpenter, 2005; Culbreth and Hairston-Strang, 2011; Eschtruth and Battles, 2009).

This study was purely observational. This meant we were unable to test more specifically which variables drive buckthorn densities; is it the fact that white pine is present, or is it because of another factor that only is present under a white pine overstory? It would be beneficial to treat a densely invaded stand against a control to try and get a better understanding of which factors are most influential. We know from Burnham and Lee (2010) that large gaps act as buckthorn sources while small gaps act as sinks. This can be applied to the harvesting plan in areas identified as good buckthorn habitat where the environmental variables cannot be changed, i.e. soil type, drainage class, historical land use. Where the features can be changed, we recommend some practices in an attempt to reduce the probability of buckthorn invasion and increase the probability of successful tree regeneration (Sec. 4.3).

Sampling effectiveness may have been limited by plot size. It is hard to accurately capture distribution of buckthorn across a forest without using a large plot size or numerous plots. If a plot happened to fall under a ‘mother’ buckthorn in an otherwise empty stand the count could be skewed.

4.3 Management recommendations

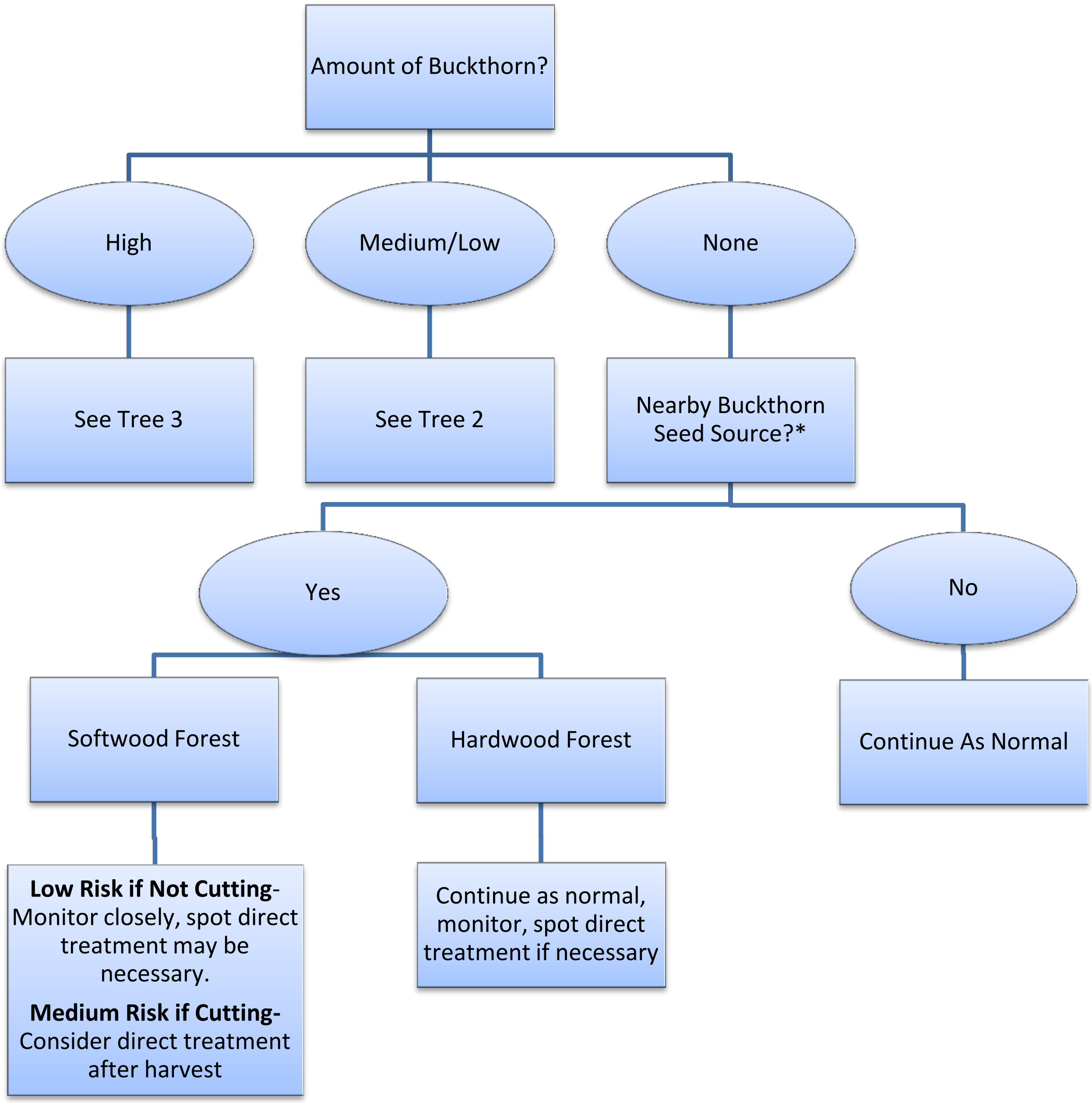
We developed a prescription risk tree to assist forest managers faced with uncertainty in the presence of buckthorn while planning a harvest (Figure 6). The prescription risk tree is based on the current knowledge about buckthorn and this research. It is meant to be a quick reference, aligning the attributes of a given forest with the variables in the guide. This is not the final word on the risk of invasion or what management should be done, it is merely a means of application of this research.

Risk is the exposure to the chance of loss as described in statistical terms (Wagner 2012). In our case we are assessing risk from the practitioners stand point, unable to support with specific statistics but with categories of low, medium, and high risk of invasion of buckthorn and inhibition of natural regeneration. The system is not site specific but is a generalization for the region where buckthorn may grow. Knowledge of the environmental variables associated with buckthorn densities should be used in conjunction with the system. Suggestions on how management should be adapted to each risk level follow the prescription risk tree.

This system is similar to the efforts of Zimmerman et al. (2011) where they suggest methods of direct control (containment, eradication, suppression) based on invasive distribution, potential ecological impact, and human values.

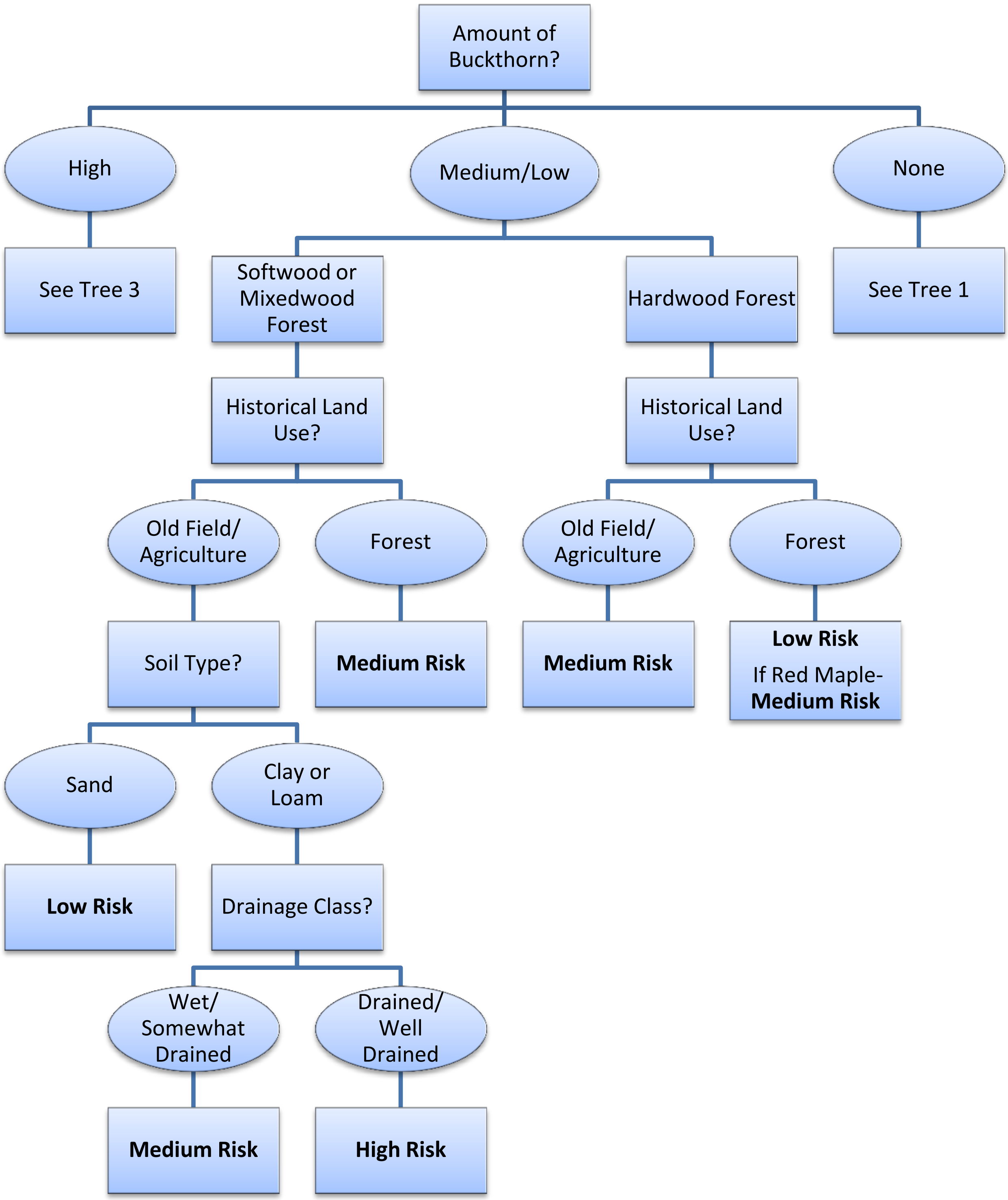
To use the tree begin by assessing the level of buckthorn in the forest in question. There are three levels of invasion; none, low/medium, and high. Once the level of invasion has been identified, move through the correlating tree. The tree will lead you though different environmental variables depending on previous choices. Once at the end of a 'branch' the tree will give a prescription risk level. Following the third tree is a list of recommendations for each risk level. These recommendations are based on data collected in this study and others.

Prescription Risk Tree 1

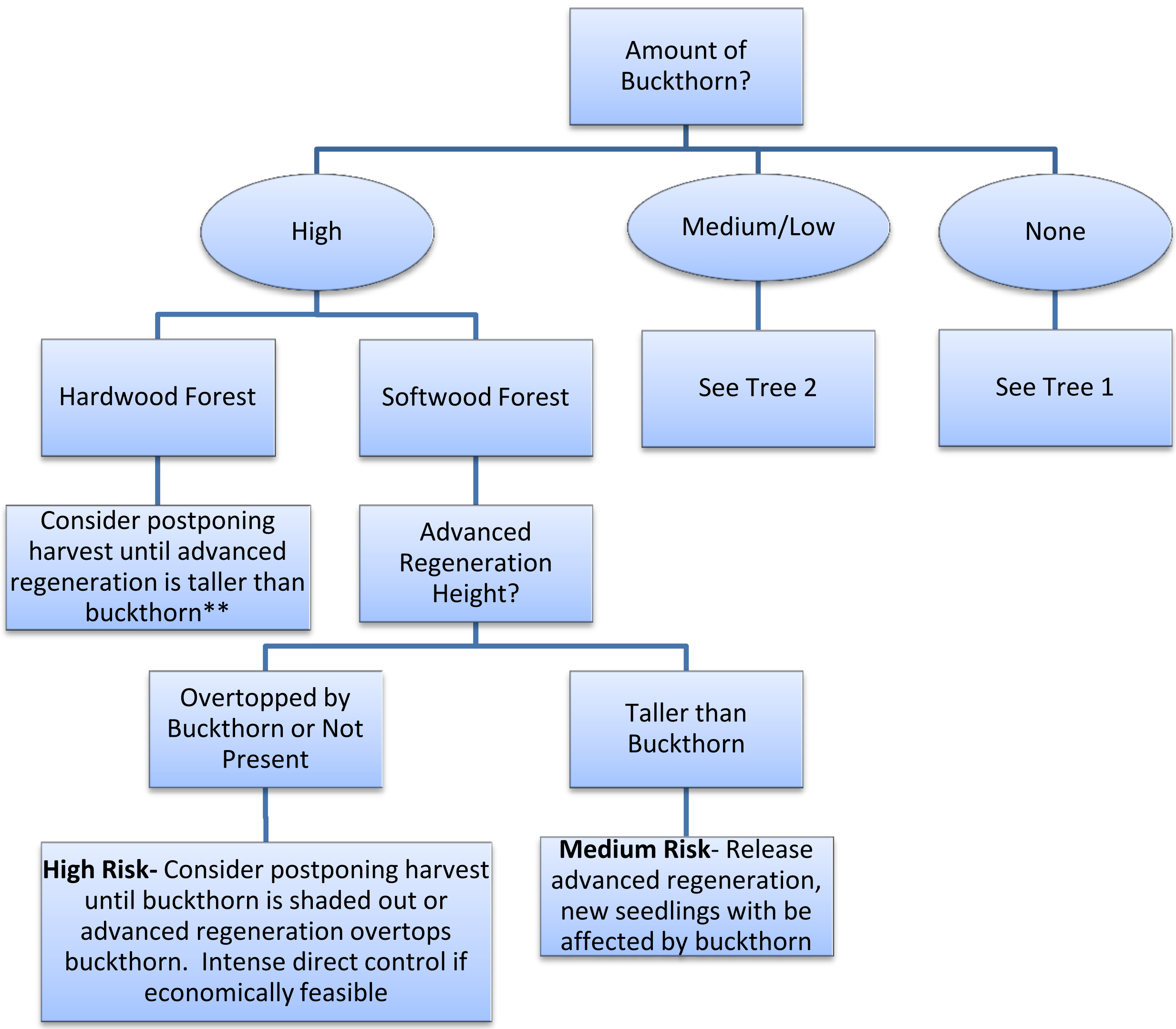


*** Proximity to seed source was not measured and therefore not defined. If a seed source of buckthorn is present within a few miles of the site in question, dispersion may be possible.**

Prescription Risk Tree 2



Prescription Risk Tree 3



**** Insufficient data for conclusions in hardwood forests with high densities of buckthorn.**

Recommendations based on risk level:

Monitoring-

- Survey site for any signs of buckthorn and remove. Focus surveys on roads, trails, boundaries, edges, and heavily disturbed sites.

Low Risk-

- Monitor, spot direct treatment if necessary.
- Avoid intense disturbance, limit number of roads and trails.

Medium Risk-

- Limit gap size, consider single tree selection.
- Release vigorous advanced regeneration.
- Limit number of roads and trails.
- Limit disturbance to soil: forwarders, winter harvest, and leave logging residue in forest to foster thicker organic layer and reduce exposed mineral soil.
- If in white pine, consider direct treatment before harvest.
- Promote hardwood regeneration using appropriate silvicultural techniques, reducing buckthorn and increase probability of regeneration survival.

High Risk-

- If cutting, expect high density of buckthorn.
- Direct control before/after harvest will be necessary or rotation will be longer.
- Consider releasing individual stems from buckthorn, 50-75 stems/acre.
- Single tree and small gaps in hardwood stands will reduce effects of buckthorn on regeneration.
- If harvesting in white pine, buckthorn will establish in any harvested area.

- Limit disturbance to soil; forwarders, winter harvest, and leave logging residue in forest to foster thicker organic layer and reduce exposed mineral soil.
- Favor advanced regeneration and fast growing species resistant to browsing such as black birch.
- If scarifying, remove seed bed entirely and bury, plant grass for erosion control, plant trees to reduce rotation time, and monitor.
- Consider delaying harvest until the buckthorn has been shaded out by the overstory or advanced regeneration has overtopped buckthorn.
- Conversion to pure hardwood using appropriate silvicultural techniques may reduce buckthorn coverage over time.

Figure 6. A prescription risk tree to aid forest managers faced with risk and uncertainty while planning a harvest in the presence of buckthorn. Three trees based on the subjective amount of buckthorn present at the time of planning; None, Medium/Low, High. Variables arranged to make using the tree efficient, not by importance of the variable; some variables are not present in the tree but in the following guide. Softwood forests are primarily white pine.

Acknowledgments

We would like to thank Steve Eisenhauer for assistance in locating UNH field sites, Trescott Company, John O'Brien and Jeffrey Smith, The Town of Durham, The Nature Conservancy, and Yale University for use of their lands.

References

Burnham, K.M., Lee, T.D., 2010. Canopy gaps facilitate establishment, growth, and reproduction of invasive Frangula alnus in a Tsuga canadensis dominated forest. Biol. Invasions 12, 1509–1520.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference. A practical information-theoretic approach. Second ed.. Springer, New York, USA.

Cappuccino, N., Carpenter, D., 2005. Invasive exotic plants suffer less herbivory than non-invasive exotic plants. Biol. Lett. 1, 435–438.

Catling, P.M., and Z.S. Porebski., 1994. The history of invasion and current status of glossy buckthorn, Rhamnus frangula, in southern Ontario. Can. Field Nat. 108, 305-310.

Chisman, H.H., Schumacher, F.X., 1940. On the tree-area ratio and certain of its applications. J. For. 38, 311–317.

Converse, C., 1984. Rhamnus cathartica and Rhamnus frangula (syn. Frangula alnus) element stewardship abstract. The Nature Conservancy, Arlington, Va., USA.

Culbreth, T., Hairston-Strang, A., 2011. Invasive species distributions and impacts on tree regeneration, Piedmont and Mountain Provinces, Maryland. Maryland Dept. of Natural Resoruces, USDA Forest Service

Cunard, C., Lee, T.D., 2009. Is patience a virtue? Succession, light, and the death of invasive glossy buckthorn (Frangula alnus). Biol. Invasions 11, 577–586.

Cygan, D., 2011. New Hampshire guide to upland invasive species. New Hampshire Department of Agriculture Markets and Food, Plant Industry Division. 3rd Edition.

Ducey, M.J., 2016. University of New Hampshire. Natural Resource and the Environment. Jan 27, 2016.

Ducey, M.J., Kershaw, J.A., 2011. Vertical Point Sampling with a Camera. North. J. Appl. For. 28, 61–65.

Ducey, M.J., R.A. Knapp., 2010. A stand density index for complex mixed species forests in the northeastern United States. Forest Ecology and Management 260: 1613-1622.

Dukes, J.S., Pontius, J., Orwig, D., Garnas, J.R., Rodgers, V.L., Brazee, N., Cooke, B., Theoharides, K. A., Stange, E.E., Harrington, R., Ehrenfeld, J., Gurevitch, J., Lerdau, M., Stinson, K., Wick, R., Ayres, M., 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? Can. J. For. Res. 39, 231–248.

Eschtruth, A.K., Battles, J.J., 2009. Acceleration of exotic plant invasion in a forested ecosystem by a generalist herbivore. Conserv. Biol. 23, 388–399.

Fagan, M.., Peart, D., 2004. Impact of the invasive shrub glossy buckthorn (Rhamnus frangula L.) on juvenile recruitment by canopy trees. For. Ecol. Manage. 194, 95–107.

Frappier, B., Eckert, R.T., Lee, T.D., 2003a. Potential impacts of the invasive exotic shrub Rhamnus frangula L. (glossy buckthorn) on forests of southern New Hampshire. Northeast. Nat. 10, 277–296.

Frappier, B., Lee, T.D., Olson, K.F., Eckert, R.T., 2003b. Small-scale invasion pattern, spread rate, and lag-phase behavior of Rhamnus frangula L. For. Ecol. Manage. 186, 1–6.

Frappier, B., Eckert, R.T., Lee, T.D., 2004. Experimental removal of the non-indigenous shrub Rhamnus frangula (glossy buckthorn): Effects on native herbs and woody seedlings. Northeast. Nat. 11, 333–342.

Hart, H.M.J., 1928. Stamtal en dunning: Een oriënteerend onderzoek naar de beste plantwijdte en dunningswijze voor den djati. Mededeelingen van het Proefstation voor het Boschwezen, No. 21, 219 p.

JMP®, Version 12.1.0. 2015. SAS Institute Inc., Cary, NC. Computer Software.

Johnson, V.S., Litvaitis, J.A., Lee, T.D., Frey, S.D., 2006. The role of spatial and temporal scale in colonization and spread of invasive shrubs in early successional habitats. For. Ecol. Manage. 228, 124–134.

Koning, C.O., Singleton, R., 2013. Effects of moderate densities of glossy buckthorn on forested plant communities in southwest New Hampshire, USA. Nat. Areas J. 33, 256–263.

Knight, K.S., Kurylo, J.S., Endress, A.G., Stewart, J.R., Reich, P.B., 2007. Ecology and ecosystem impacts of common buckthorn (Rhamnus cathartica): A review. Biol. Invasions 9, 925–937.

Lee, T.D., Eisenhauer, S.E., Gaudreau, I., In Prep. Pre-logging treatment of invasive glossy buckthorn (Frangula alnus Mill.) reduces buckthorn abundance and promotes regeneration of eastern white pine (Pinus strobus L.). University of New Hampshire, Durham, NH

Lee, T.D., Thompson, J.H., 2012. Effects of logging history on invasion of eastern white pine forests by exotic glossy buckthorn (Frangula alnus P. Mill.). For. Ecol. Manage. 265, 201–210.

Lundgren, M.R., Small, C.J., Dreyer, G.D., 2004. Influence of land use and site characteristics on invasive plant abundance in the Quinebaug Highlands of southern New England. Northeast. Nat. 11, 313–332.

MATLAB R2015b. 2015. The MathWorks, Inc., Natick, Massachusetts, United States. Computer Software

Nobis, M., Hunziker, U., 2005. Automatic thresholding for hemispherical canopy-photographs based on edge detection. Agric. For. Meteorol. 128, 243–250.

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecological Monographs 76, 521–547.

Olson, E., Kenefic, L.S., Dibble, A.C., Brissette, J.C., 2011. Nonnative invasive plants in the Penobscot Experimental Forest in Maine, USA: Influence of site, silviculture, and land use history. J. Torrey Bot. Soc. 138, 453–464.

Orr, S.P., Rudgers, J.A., Clay, K., 2005. Invasive plants can inhibit native tree seedlings: Testing potential allelopathic mechanisms. Plant Ecol. 181, 153–165.

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Stout, S. L., Nyland, R. D., 1986. Role of species composition in relative density measurement in Allegheny hardwoods. Can. J. For. Res. 16: 574-579.

Stout, S. L., Marquis, D. A., Ernst, R. L., 1987. A relative density measure for mixed-species stands. J. For. 7: 45-47.

Wagner, J.E., 2012. *Forest Economics: A Managerial Approach*. Abingdon, Oxon: Routledge. Print.

Wear, D.N., Greis, J.G., 2002. Southern forest resource assessment: summary report. Gen. Tech. Rep. SRS-54. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 103 p.

Webster, C.R., Jenkins, M.A., Jose, S., (2006) Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. J Forest 104(7), 366–374.

Williams, C.E., Krock, S.L., 2012. Patchy invasion of riparian savannas by Rhamnus frangula L. (Rhamnaceae) in northwestern Pennsylvania: Is soil drainage a factor? Castanea 77, 318–326.

Wilson, F.G., 1946. Numerical expression of stocking in terms of height. J. For. 44: 758-761.

Yamasaki, M., 2003. White pine as wildlife habitat. Managing white pine a new millennium. 2003 workshop proceedings.

Zimmerman, C., Jordan, M., Sargis, G., Smith, H., Schwager, K., 2011. An invasive plant management decision analysis tool. Version 1.1. The Nature Conservancy, Arlington, Virginia.

CHAPTER III

Conclusion

Glossy buckthorn is clearly associated with several of the variables sampled. It was found in its highest density under disturbed white pine forests originating from old fields with thin organic layers and low herbaceous cover, on drained loamy soils. Lowest densities of glossy buckthorn were associated with hardwood forests that have historically been forested with thick organic layers, high herbaceous cover, and on sandy soil. Most forest types with a white pine component had high levels of buckthorn, unless it was a white pine and eastern hemlock forest. Red maple and red oak both had elevated levels of buckthorn as compared to other hardwood forest types. Canopy cover and basal area are not associated with buckthorn density. These observations were statistically tested using generalized linear models with a Poisson distribution. The most influential variables found in the generalized linear model were: organic layer thickness, dominant overstory species, percent herbaceous cover, drainage class, soil type, historical land use, and evidence of harvest.

Softwood forests had overall higher average of buckthorn stems than hardwood forests. The relationships between buckthorn numbers and the variables were much more defined in softwood forests. These stronger relationships may make indirect management easier in softwood forests. Buckthorn levels decreased as organic layer thickness increased in softwood forests, but this was opposite in hardwood forests.

Average shade tolerance of native regeneration is not affected by the presence of buckthorn. Regeneration is the result of the historical environment, possibly before buckthorn or as the result of a disturbance. There is evidence of direct competition between buckthorn and native regeneration. They seem to be competing for similar resources. When there is a high relative spacing of buckthorn there is a low relative spacing of regeneration, and vice versa.

This study was limited in that it was purely observational. We were unable to experiment with the specific factors that may limit or promote buckthorn growth. The average shade tolerance of regeneration may not accurately represent what is happening with the regeneration in the presence of buckthorn. We counted each stem from seedling to a dbh less than 3in. This does not tell us what stems are surviving unless we were to separate by which stems overtopped buckthorn. Our attempt to do this was by using relative spacing values. The average shade tolerance value would not be very influenced if a few species with shade tolerance extremes were present due to the small range of possible values (0-5). We suggest that further research be focused on experimental testing of which factors truly drive buckthorn density based on these findings.

References

Burnham, K.M., Lee, T.D., 2010. Canopy gaps facilitate establishment, growth, and reproduction of invasive Frangula alnus in a Tsuga canadensis dominated forest. Biol. Invasions 12, 1509–1520.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference. A practical information-theoretic approach. Second ed.. Springer, New York, USA.

Cappuccino, N., Carpenter, D., 2005. Invasive exotic plants suffer less herbivory than non-invasive exotic plants. Biol. Lett. 1, 435–438.

Catling, P.M., and Z.S. Porebski., 1994. The history of invasion and current status of glossy buckthorn, Rhamnus frangula, in southern Ontario. Can. Field Nat. 108, 305-310.

Chisman, H.H., Schumacher, F.X., 1940. On the tree-area ratio and certain of its applications. J. For. 38, 311–317.

Converse, C., 1984. Rhamnus cathartica and Rhamnus frangula (syn. Frangula alnus) element stewardship abstract. The Nature Conservancy, Arlington, Va., USA.

Culbreth, T., Hairston-Strang, A., 2011. Invasive species distributions and impacts on tree regeneration, Piedmont and Mountain Provinces, Maryland. Maryland Dept. of Natural Resoruces, USDA Forest Service

Cunard, C., Lee, T.D., 2009. Is patience a virtue? Succession, light, and the death of invasive glossy buckthorn (Frangula alnus). Biol. Invasions 11, 577–586.

Cygan, D., 2011. New Hampshire guide to upland invasive species. New Hampshire Department of Agriculture Markets and Food, Plant Industry Division. 3rd Edition.

Ducey, M.J., 2016. University of New Hampshire. Natural Resource and the Environment. Jan 27, 2016.

Ducey, M.J., Kershaw, J.A., 2011. Vertical Point Sampling with a Camera. North. J. Appl. For. 28, 61–65.

Ducey, M.J., R.A. Knapp., 2010. A stand density index for complex mixed species forests in the northeastern United States. Forest Ecology and Management 260: 1613-1622.

Dukes, J.S., Pontius, J., Orwig, D., Garnas, J.R., Rodgers, V.L., Brazee, N., Cooke, B., Theoharides, K. A., Stange, E.E., Harrington, R., Ehrenfeld, J., Gurevitch, J., Lerdau, M., Stinson, K., Wick, R., Ayres, M., 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? Can. J. For. Res. 39, 231–248.

Eschtruth, A.K., Battles, J.J., 2009. Acceleration of exotic plant invasion in a forested ecosystem by a generalist herbivore. Conserv. Biol. 23, 388–399.

Evans, C.W., Moorhead, D.J., Bargeron, C.T., Douce, G.K., 2006. Invasive plant responses to silvicultural practices in the south. The University of Georgie BUgwood network, Tifton GA, BW-2006-03. 52 p.

Fagan, M.., Peart, D., 2004. Impact of the invasive shrub glossy buckthorn (Rhamnus frangula L.) on juvenile recruitment by canopy trees. For. Ecol. Manage. 194, 95–107.

Frappier, B., Eckert, R.T., Lee, T.D., 2003a. Potential impacts of the invasive exotic shrub Rhamnus frangula L. (glossy buckthorn) on forests of southern New Hampshire. Northeast. Nat. 10, 277–296.

Frappier, B., Lee, T.D., Olson, K.F., Eckert, R.T., 2003b. Small-scale invasion pattern, spread rate, and lag-phase behavior of Rhamnus frangula L. For. Ecol. Manage. 186, 1–6.

Frappier, B., Eckert, R.T., Lee, T.D., 2004. Experimental removal of the non-indigenous shrub Rhamnus frangula (glossy buckthorn): Effects on native herbs and woody seedlings. Northeast. Nat. 11, 333–342.

Hart, H.M.J., 1928. Stamtal en dunning: Een oriënteerend onderzoek naar de beste plantwijdte en dunningswijze voor den djati. Mededeelingen van het Proefstation voor het Boschwezen, No. 21, 219 p.

Jenkins, M.A., Parker, G.R., 2000. The response of herbaceous-layer vegetation to anthropogenic disturbance in intermittent stream bottomland forests of southern Indiana, USA. Plant Ecol. 151, 223–237.

JMP®, Version 12.1.0. 2015. SAS Institute Inc., Cary, NC. Computer Software.

Johnson, V.S., Litvaitis, J.A., Lee, T.D., Frey, S.D., 2006. The role of spatial and temporal scale in colonization and spread of invasive shrubs in early successional habitats. For. Ecol. Manage. 228, 124–134.

Koning, C.O., Singleton, R., 2013. Effects of moderate densities of glossy buckthorn on forested plant communities in southwest New Hampshire, USA. Nat. Areas J. 33, 256–263.

Knight, K.S., Kurylo, J.S., Endress, A.G., Stewart, J.R., Reich, P.B., 2007. Ecology and ecosystem impacts of common buckthorn (Rhamnus cathartica): A review. Biol. Invasions 9, 925–937.

Lee, T.D., Eisenhauer, S.E., Gaudreau, I., In Prep. Pre-logging treatment of invasive glossy buckthorn (Frangula alnus Mill.) reduces buckthorn abundance and promotes regeneration of eastern white pine (Pinus strobus L.). University of New Hampshire, Durham, NH

Lee, T.D., Thompson, J.H., 2012. Effects of logging history on invasion of eastern white pine forests by exotic glossy buckthorn (Frangula alnus P. Mill.). For. Ecol. Manage. 265, 201–210.

Luginbuhl, J.M., Green, J.T., Poore, M.H., Mueller, J.P., 1996. Use of goats as biological agents for the control of unwanted vegetation. NC State University. College of Agriculture and Life Sciences.

Lundgren, M.R., Small, C.J., Dreyer, G.D., 2004. Influence of land use and site characteristics on invasive plant abundance in the Quinebaug Highlands of southern New England. Northeast. Nat. 11, 313–332.

MATLAB R2015b. 2015. The MathWorks, Inc., Natick, Massachusetts, United States. Computer Software

Nobis, M., Hunziker, U., 2005. Automatic thresholding for hemispherical canopy-photographs based on edge detection. Agric. For. Meteorol. 128, 243–250.

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecological Monographs 76, 521–547.

Olson, E., Kenefic, L.S., Dibble, A.C., Brissette, J.C., 2011. Nonnative invasive plants in the Penobscot Experimental Forest in Maine, USA: Influence of site, silviculture, and land use history. J. Torrey Bot. Soc. 138, 453–464.

Orr, S.P., Rudgers, J.A., Clay, K., 2005. Invasive plants can inhibit native tree seedlings: Testing potential allelopathic mechanisms. Plant Ecol. 181, 153–165.

R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reichard, S.E., 1997. Prevention of invasive plant introductions on national and local levels. Assess. Manag. Plant Invasions 215–227.

Reichard, S., White, P., 2001. Horticulture as pathways of plant introductions in the United States. Am. Inst. Biol. Sci. 51, 103–113.

Stokdyk, J.P., Herrman, K.S., 2014. Short-Term Impacts of Frangula alnus litter on forest soil properties. Water, Air, Soil Pollut. 225, 2000.

Stout, S. L., Nyland, R. D., 1986. Role of species composition in relative density measurement in Allegheny hardwoods. Can. J. For. Res. 16: 574-579.

Stout, S. L., Marquis, D. A., Ernst, R. L., 1987. A relative density measure for mixed-species stands. J. For. 7: 45-47.

Wagner, J.E., 2012. *Forest Economics: A Managerial Approach*. Abingdon, Oxon: Routledge. Print.

Wear, D.N., Greis, J.G., 2002. Southern forest resource assessment: summary report. Gen. Tech. Rep. SRS-54. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 103 p.

Webster, C.R., Jenkins, M.A., Jose, S., (2006) Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. J Forest 104(7), 366–374.

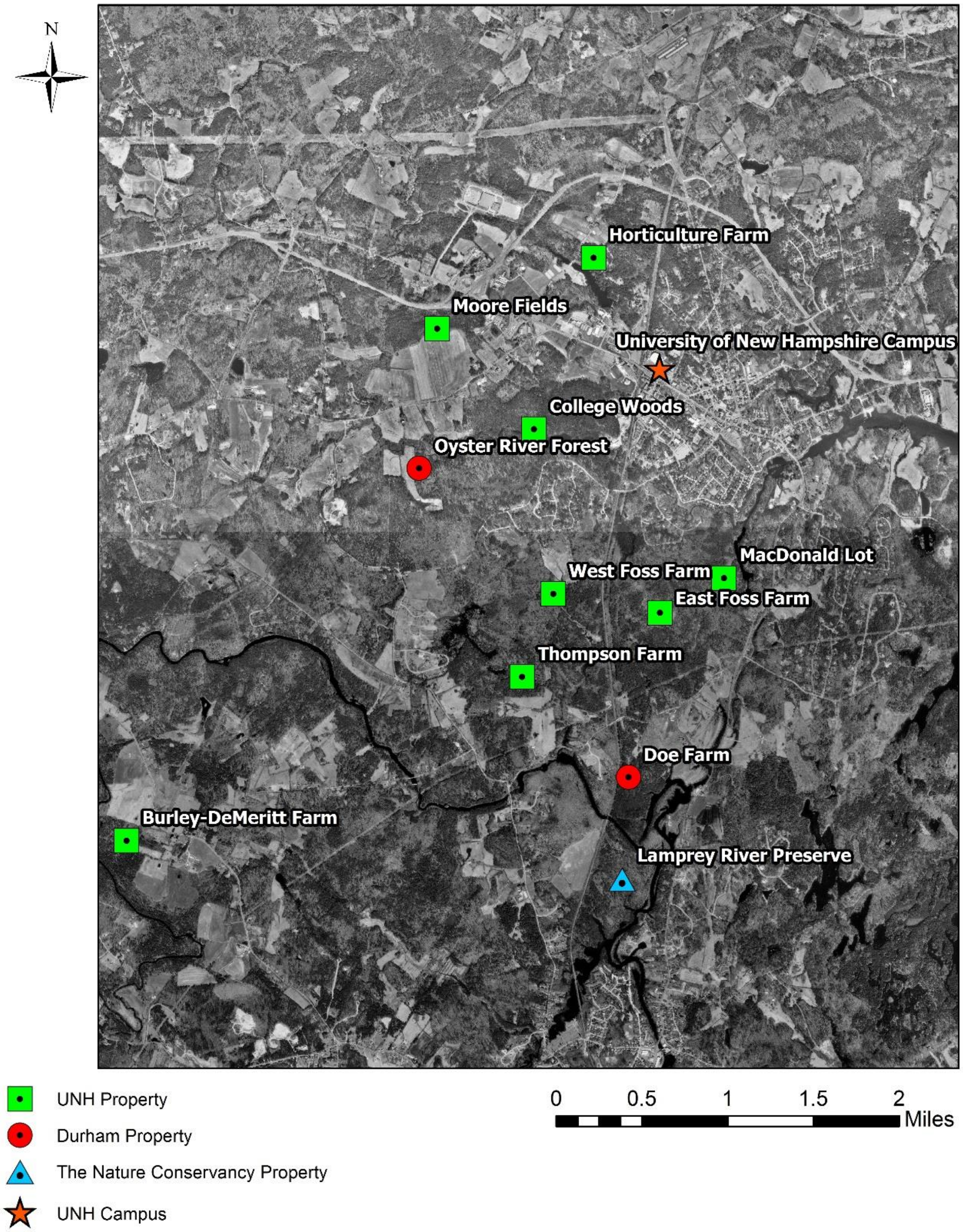
Williams, C.E., Krock, S.L., 2012. Patchy invasion of riparian savannas by Rhamnus frangula L. (Rhamnaceae) in northwestern Pennsylvania: Is soil drainage a factor? Castanea 77, 318–326.

Wilson, F.G., 1946. Numerical expression of stocking in terms of height. J. For. 44: 758-761.

Yamasaki, M., 2003. White pine as wildlife habitat. Managing white pine a new millennium. 2003 workshop proceedings.

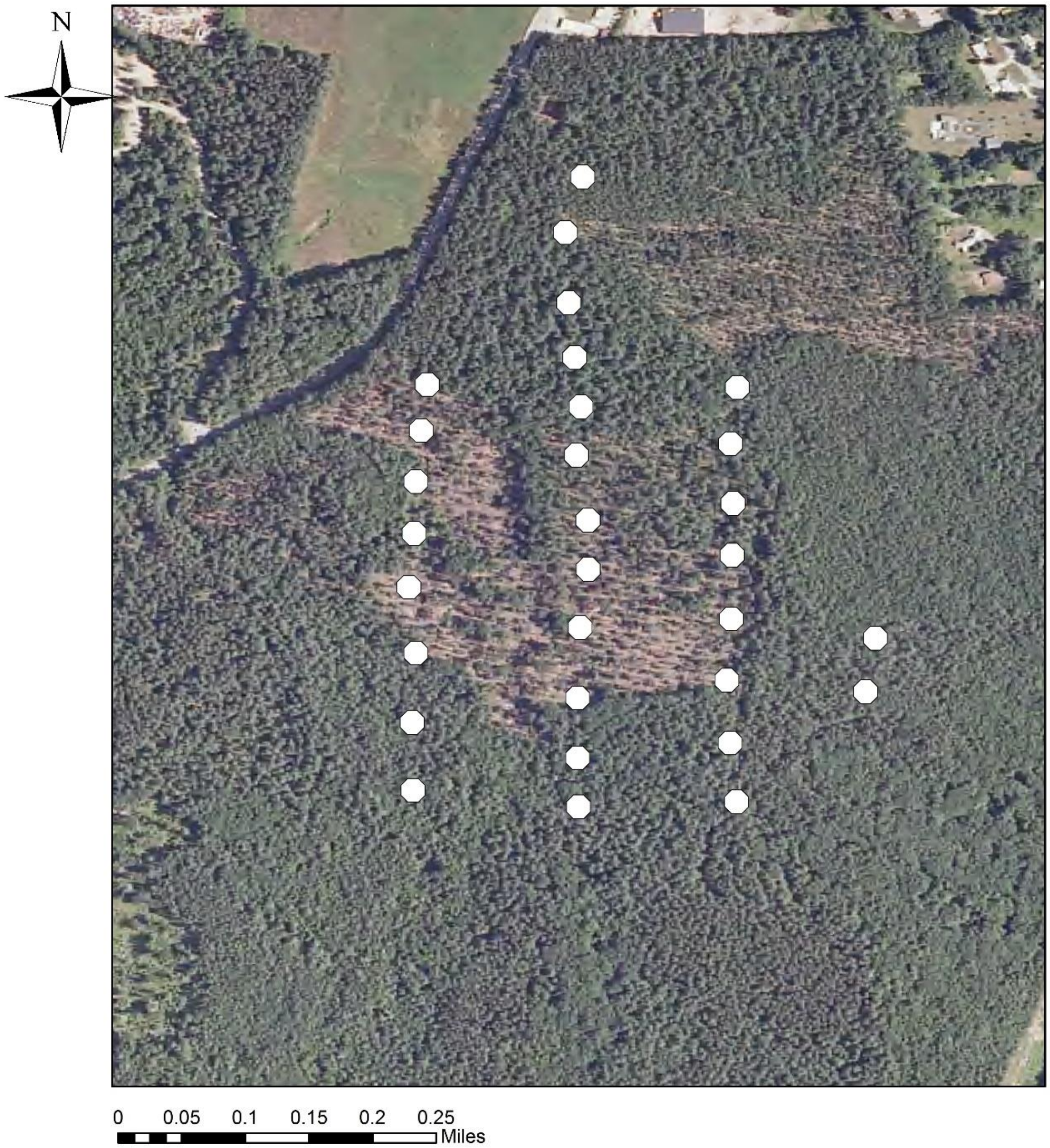
Zimmerman, C., Jordan, M., Sargis, G., Smith, H., Schwager, K., 2011. An invasive plant management decision analysis tool. Version 1.1. The Nature Conservancy, Arlington, Virginia.

Appendix A



Map of sampling properties at the UNH/Durham location

Appendix B



Sampling plot locations at the Yale-Toumey Forest in Keene and Swanzey, NH.

Appendix C

List of Dominant Overstory Species

- Aspen
- Aspen/Red Maple
- Beech
- Hemlock
- Hemlock/White Pine
- Mixed Hardwood
- Hardwood/White Pine
- Norway Spruce
- Oak
- Red Maple
- Red Maple/Hemlock
- Red Maple/Red Oak
- Red Maple/Sugar Maple
- Red Maple/White Pine
- Red Oak
- Red Oak/Hemlock
- Red Oak/Red Maple
- Red Oak/ Sugar Maple
- Red Oak/White Pine
- Red Pine
- Red Pine/Sugar Maple
- Sweet Birch/Aspen
- Shagbark Hickory
- Sugar Maple
- Sugar Maple/Hemlock
- White Oak
- White Pine
- White Pine/American Elm
- White Pine/Aspen
- White Pine/Beech
- White Pine/Hemlock
- White Pine/Red Maple
- White Pine/Red Oak
- White Pine-Dense Beech Understory
- White Pine-Dense Hardwood Understory